

ADAPTIVE CONVERGENCES IN TWO NESTLING BIVALVES (MYOIDAE: MYIDAE, HIATELLIDAE) OF THE BRAZILIAN LITTORAL

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ABSTRACT

The myoideans bivalves *Hiatella solida* (Sowerby, 1834) (Hiatellidae) and *Sphenia antillensis* Dall & Simpson, 1901 (Myidae) from the littoral of São Paulo, Brazil, are studied. Both species normally live as nestling forms and share the same habitat. *S. antillensis* was found in the southern littoral of São Paulo, Brazil, many years after the record of *H. solida* in the area. The habit of living byssally attached inside hollows and crevices and submitted to the same environmental conditions may have led to the evolution of adaptive convergence and the appearance of similarities responsible for misunderstandings concerning the identification of both species when in their natural habitat or in a mixed collection of their shells. A comparative analysis of the shell features and of the anatomy of the soft parts revealed some of these similarities, as well as distinctive characteristics which are specially centered in the hinge line, siphons and alimentary canal, all of them pointed out and illustrated.

KEYWORDS. *Hiatella solida*, *Sphenia antillensis*, nestling bivalves, adaptive convergence, Brazilian littoral.

INTRODUCTION

The evolutionary history of bivalves has many examples of adaptive convergence, a phenomenon responsible for the existence of nonrelated species having a high degree of similarities. Very close resemblance has led to misidentifications and/or to overlooking species in their habitat, postponing their discovery and study.

Collecting bivalves in the littoral of São Paulo, Brazil, NARCHI (1973) picked out and studied *Hiatella solida* (Sowerby, 1834) (Hiatellidae), frequently found as a solitary byssiferous or nestling form in the intertidal zone. The species was found in cavities within sandy blocks constructed by the polychaete worm *Phragmatopoma lapidosa* Kinberg, 1867 together with *Petricola (Rupellaria) typica* (Jonas, 1844) and another sympatric Petricolidae species, initially identified as *Petricola pholadiformis* Lamarck, 1818.

Along with the study of the functional morphology of *Hiatella solida*, Narchi started

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the analysis of *Petricola (Rupellaria) typica* (NARCHI, 1974), and of the sympatric Petricolidae. A careful observation of the latter bivalve revealed that its siphons were quite different from those described and drawn by PURCHON (1955) for *P. pholadiformis* and its shell disclosed further differences which convinced NARCHI (1975) to describe the material as a new species, *Petricola stellae*. In this work Narchi has shown how the similarities among these Petricolidae species have led Brazilian malacologists to identify the new species erroneously as *P. pholadiformis*. Only the accurate insight of an expert could detect such minor differences among so closely related species, very similar owing to their similar genotype and submitted to the same selective pressures of the environment.

Later the authors of the present paper returned to the same places where Narchi had found all the formerly mentioned species and verified the presence of *Sphenia antillensis* Dall & Simpson, 1901, which was studied (NARCHI & DOMANESCHI, 1993) in its morphological and functional aspects. This species is the only member of the Myidae inhabiting Brazilian waters, and has a similar habit to that of *Hiatella solida*. According to RIOS (1994), *S. antillensis* has the littoral of Santa Catarina as its southern limit of distribution.

The present paper points out and compare similarities and mainly the distinctive shell and anatomical features of these two myoideans species, in order to discuss the reasons which may led to overlook *S. antillensis* in the studied area despite its occurrence together with *H. solida*.

MATERIAL AND METHODS

Living specimens of *Hiatella solida* and *Sphenia antillensis*, shell length of both species varying from 3 to 12mm were collected on beaches in Santos and São Vicente (23°58'S; 46°22'W), São Paulo, Brazil, from June, 1993 to May, 1994. They were found attached by byssus threads to the colonial ascidian *Polyandrocarpa zorritensis* (Van Name, 1931), which usually grows in clumps of hundreds of animals which cover boulders in the low intertidal zone. Both species also occur among tubes of the polychaete *Phragmatopoma lapidosa*, which are grouped in masses sometimes of several feet, composed entirely of sand and so firm as to be like a honeycombed porous sandstone, as well as among the byssal tangle of the mytilid bivalve *Perna perna* (Linnaeus, 1758), and among branched algae and bryozoans. Another common habitat for the species was the crevices and burrows in hard substrata and burrows constructed by other invertebrates, which provide shelter and protection against the direct wave action.

Living specimens were maintained in aquarium and Petri dishes containing clean, aerated sea water at room temperature (~21°C). In such conditions they survive up to seven weeks. Drawings of live and preserved specimens were made. Magnesium sulphate was used to anaesthetize the animals.

Specimens obtained on the studied area were deposited at the Museu de Zoologia, Universidade de São Paulo (MZSP), under the numbers (MZSP n°28.813) for *Hiatella solida* and (MZSP n° 28.814) for *Sphenia antillensis*.

RESULTS

Shell. Juveniles and adults of *H. solida* and *S. antillensis*, of all classes of size shares many similarities. The specimens studied were mainly white, quite irregular in shape and outline, and in a same species rarely two specimens were alike. The shell is inequilateral and inequivalue with the umbos in the anterior half directed inwards. The outer surface is covered with a yellowish periostracum haphazardly eroded and the sculpture consisting of concentric lines and undulations which are sometimes irregular. The inside of the shell is opaque or glossy white with the pallial line and pallial sinus inconspicuous.

Search for different features in the shell of the two species may specially be led to the hinge region (figs. 1 - 4). *Hiatella solida* can be recognized by its external and conspicuous ligament arising immediately posterior to the umbos (fig. 1) and an undulating hinge line with one short projecting cardinal tooth in each valve, the left valve with two additional smaller teeth; both or one of these last teeth almost always worn away in old shells (fig. 3). *Sphenia antillensis* is characterized by the absence of hinge teeth and by the possession of an internal ligament attached to an elongated, flattened and projecting chondrophore on the left valve and to a nearly oval excavation with a ridge-like ventral margin under the umbo in the right valve (figs. 2, 4). Comparatively the shell valves of *Hiatella* are stronger, better calcified and better adapted to support mechanical erosion.

Specimens growing free from the constraint of a hollow or crevice (ex.: among branched algae and bryozoans) generally have more regular shells, although no two specimens are alike. These regular shells tend to be rectangular in outline and gap posteriorly in *H. solida*. In *S. antillensis* an ovaled outline predominates; this can be slightly modified to a rectangular outline in specimens with a sharp posterior truncation. The rear end in *Sphenia* is weakly calcified and gapes slightly. These features may not be so conspicuous in nestling specimens. Very distorted shells predominate among specimens living in crevices, cavities and among the byssal tangle of mytilids. HUNTER (1949) stated that the genus *Hiatella* as a whole exhibits great variation in the shell form. Severe distortions caused by conformity to crevices and burrows in which *H. solida* and *S. antillensis* settled may produce such anomalous shells that they require the attention of experts for their identification.

Mantle. The mantle shows great similarities in both species. Their free edges are united except for the two siphonal orifices and for a small pedal aperture, with the fusion involving the inner and middle folds, as well the periostracal grooves (NARCHI, 1973; NARCHI & DOMANESCHI, 1993). As described by YONGE (1951a) for *Sphenia binghami*, the mantle tissues exposed ventrally when the valves separate are everywhere covered with periostracum.

Siphons. The siphons of both species are similar in the way they are formed (type C of YONGE, 1948; 1982) and in relation to the presence of siphonal apertures fringed with an inner and an outer row of simple tentacles, the opening of the exhalant one showing in addition a small tubular membrane (figs. 5, 6). In both species these organs are fused together, surrounded by periostracum and show sensitivity to mechanical and luminous stimuli.

Despite their great similarities the siphons when fully extended provide additional and secure resources to distinguish *Hiatella* from *Sphenia*: those of *Hiatella* have their basal halves fused together and the distal ones are free, widely separated and the organs are as long as or longer than the shell (fig. 5), while those of *Sphenia* are completely fused, not attaining half of the shell length (fig. 6). Besides these, the siphons of *Hiatella* are very attractive because of their bright orange-yellow color with pigmented darker tips, contrary to those of *Sphenia* which only have a brownish color becoming darker in the direction of the tips.

The presence of simple tentacles around the siphonal apertures and the degree of sensitivity of the siphons to mechanical and luminous stimuli as registered by NARCHI

(1973) and NARCHI & DOMANESCHI (1993) for *H. solida* and *S. antillensis* respectively, contrasted with the observations of NARCHI (1974; 1975) for *Petricola (Rupellaria) typica* and *P. stellae*, respectively, which have high sensitive siphons with a complex of ramified tentacles, despite the fact that these two last species share the same habitat together with *Hiatella* and *Sphenia*.

Mantle cavity. The organs and their disposition in the mantle cavity are similar in both species so that specific identification by observing the soft parts requires careful examination of some anatomical peculiarities.

Owing to the greater portion of the shell being posterior to the hinge and umbos, the organs and structures are better developed in that region, giving a striking asymmetry between the anterior and posterior regions of the body, a feature very common among bivalves which retain a well-developed byssal apparatus (YONGE, 1962).

The adductor muscles of *H. solida* and *S. antillensis* share the peculiarity of being not aligned; the semilunate anterior adductor is displaced ventrally and is comparatively smaller than the posterior one which is ovate to semi-orbicular in cross section (figs. 9, 10).

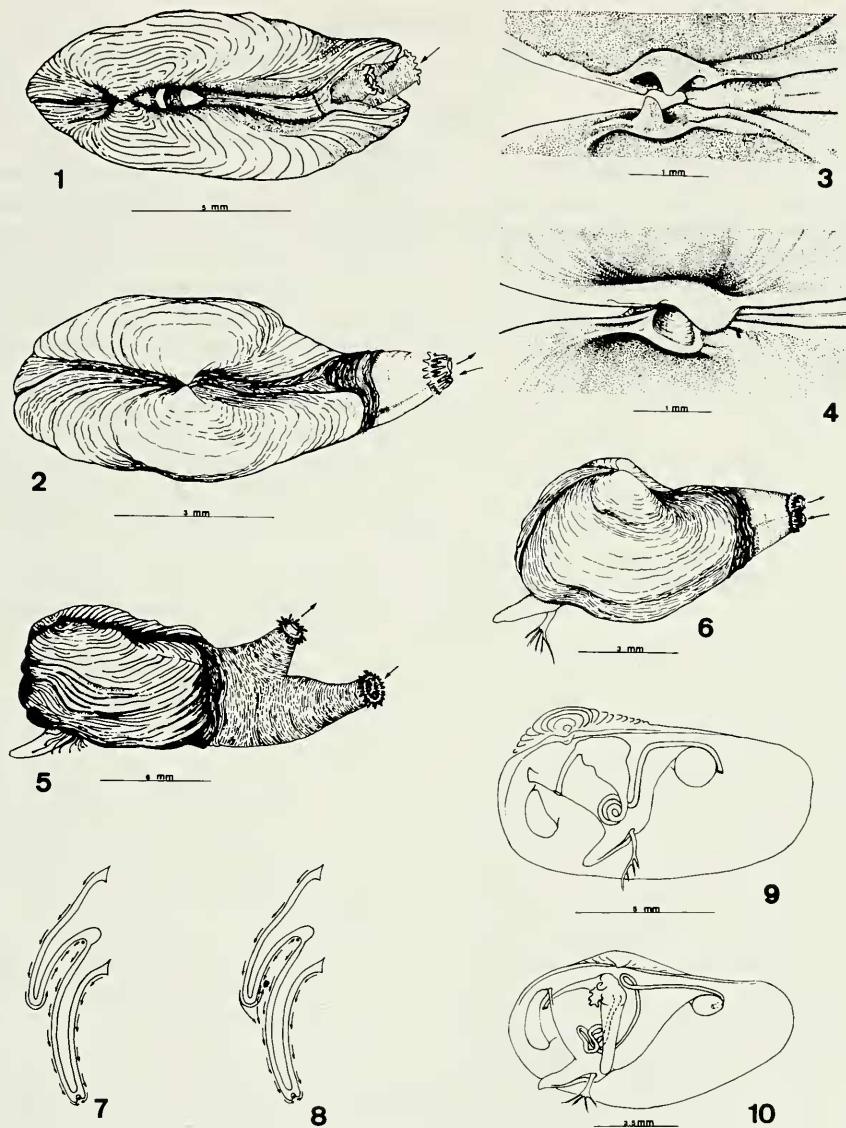
The foot is short, finger-shaped and though doubtless capable of enabling the adult animal to move, its principal function is to attach the byssus threads to the substratum. The byssal groove extends almost the entire length of the ventral surface of the foot (figs. 9, 10). The byssal gland lies posteriorly inside the heel of the foot reached by the pedal muscles. The byssus threads are joined together at their basal region forming a ramified stalk. According to YONGE (1962), the retention of a functional small byssal apparatus is associated with the habit of nestling in some species of Myoidea and Saxicavoidea [= Hiatelloidea] and it has had a major effect on the form of the animal.

The ctenidia of both species are long and moderately narrow. The demibranchs are flat and homorhabdic; the outer demibranch has a short supraxial extension and the inner demibranch is the only one to bear a marginal food groove (figs. 7, 8). Minor differences among the ctenidia are concerned with their functional anatomy; the ciliary currents are of type C of ATKINS (1937) in *H. solida* (fig. 7) and of type C₁ of ATKINS (1937) in *S. antillensis* (fig. 8).

The labial palps are small in relation to the ctenidia; the association between them belongs to the category III of STASEK (1963). The labial palps bear few plicae and have an intensive muscular activity and can roll up very easily if the quantity of particles is excessive. Large ctenidia and small labial palps are characteristic of bivalves with a suspension feeding habit.

Alimentary canal. The general configuration of the alimentary canal is similar in both species (figs. 9, 10). The esophagus enters dorsally in the anterior part of the stomach; the midgut is short and after a series of tight spiral curves, or loops, near and anterior to the distal end of the style-sac, it turns abruptly backwards, ascends posteriorly to the right side of the style-sac onto the dorsal region of the visceral mass. Here the hindgut turns backwards, traverses the pericardium, embraces the posterior adductor muscle and ends up in the anal papilla on the posterior side of this muscle in *Hiatella*, and ventrally in *Sphenia*.

Despite the great similarity between the alimentary canal of *H. solida* and that of *S. antillensis*, this system provides two major features which easily distinguish both species from each other: the style-sac and the midgut are joined together in *Hiatella* (fig. 9) while in *Sphenia* they are completely separated (fig. 10) as in all other known Myidae; the stomach in *H. solida*



Figs. 1 - 10. *Hiatella solida* (figs. 1, 3, 5, 7, 9); *Sphenia antillensis* (figs. 2, 4, 6, 8, 10). 1, 2: dorsal view of live specimens showing the conspicuous external ligament in *Hiatella*, not visible in *Sphenia* where it is completely internal; 3, 4: internal view of the shell (left valve at the top) showing details of the hinge line. 5, 6, left lateral view of live specimens showing extended siphons and foot. Arrows: direction of the inhalant and exhalant currents. 7, 8: diagrammatic transverse section showing the form of the ctenidium and the direction of the frontal currents. Solid circles, oralwards currents; dotted circle, vortex of particles between inner and outer demibranchs. 9, 10: course of the alimentary canal. (Figs. 1, 3, 5 redrawn after NARCHI, 1973; 8, after NARCHI & DOMANESCHI, 1993; 9, adapted from NARCHI, 1973; 10: NARCHI & DOMANESCHI, 1993).

is of type IV in the classification of PURCHON (1958) and in *S. antillensis* it is of type V in the classification of PURCHON (1960).

DISCUSSION

Hiatella solida is the only species of the genus represented in Brazilian waters (NARCHI, 1973). Its occurrence in the intertidal zone of the littoral of São Paulo, Brazil, mainly attached by byssus threads inside hollows and crevices corroborates the statement of KEEN (1971) about its nestling habit. HUNTER (1949) considered the British species of *Hiatella* mainly rockboring in habit with non-boring forms in the same species. TEBBLE (1976) observed that *Hiatella arctica* (Linnaeus, 1767) from the British coast lives as a nestler in holes in rocks offshore or as a borer in very soft rocks, but considered the species as much a nestler as a borer.

Sphenia antillensis is the only *Myidae* inhabiting Brazilian seas. The *Myidae* are interesting because of the considerable variety of forms and habits of its species. Nestling, commensals, borers in soft rocks and deep burrowers are known mainly from the works of YONGE (1923; 1951a; 1951b; 1951c; 1982). *Sphenia binghami* Turton, 1822 is a British species often found within crevices, specially those formed or else increased in size by *Hiatella* in stones or shells (YONGE, 1951a).

The small size of the adult forms of *Hiatella* and particularly of *Sphenia* seems to have been of adaptive value, since it allows to these animals to explore very restricted spaces inside skeletal structures of dead organisms, holes bored and occupied previously by borer species, crevices in rocks and very restricted spaces among gregarious, colonial or branched organisms as well as among byssus threads of other bivalves.

HUNTER (1949) showed that settled post-larvae of *Hiatella* searched for irregular pits or crevices in firm substrata where they preferentially attach, with the juveniles growing as borer or non-boring (nestler) forms, a behavior determined by the nature of the substratum. According to KEEN (1971), *Hiatella* is a nestler and its larvae float into crevices where they grow up to fit the contours of the cavity and no two shells are the same shape; hence, there is difficulty in deciding whether only one worldwide species is present or whether several separate species of the genus can be isolated.

The byssal threads are an essential agent of stability during metamorphosis of the post-larva. In species where the adoption of the final adult habit is slow, the byssus is retained for a relatively long time, permitting the fixation of the young mobile bivalve for variable periods of time. In adults they are generally employed to secure the animal against powerful water movements such as tidal currents or waves, resulting in a massive structure with a major influence on the form of the animal (YONGE, 1962).

Retention of a small but functional byssal apparatus throughout the animal life may have contributed to the evolution of the nestling habit of *Hiatella* and *Sphenia*, once the byssus threads play an important role in the survival of these animals. The "complex protective reaction", well observed and described by HUNTER (1949) for British species of *Hiatella* seems to constitute a strong evidence of the adaptive value of the byssus for the adult forms. Mechanical and shadowing stimulation of the siphons induces non-boring forms of *Hiatella* to retract the foot and byssus, pulling themselves down on to the substratum. Closure of the pedal and siphonal apertures precedes the retraction of the siphons. Once the adductors do not contract, nor water is expelled, withdrawal of the siphons increases the water pressure in the

mantle cavity and the shell valves move apart. In the normal habitat of crack or crevice this protective reaction results in a tight wedging of the shell against the sides (HUNTER, 1949). Evidently such behavior difficults predatory actions or the removal of the specimen if exposed to a sudden and powerful water movement.

HUNTER (1949) had observed that in borer forms of *Hiatella* the byssal gland and byssal groove are prominent but the byssus is laid down only when the borer is removed from its burrow or disturbed after the removal of one wall of its burrow. In a normal condition such borers may occasionally be found with a single byssus thread attached to the wall of the burrow, probably the byssus being used to alter the position of the animal in the burrow. According to Hunter protective reactions in borers result in the contraction of the siphons with their laterally expanded walls being closely applied to the walls of the burrow, providing a fixed point around which the body and shell valves can move in the process of perforation of the substratum.

The predominance of distorted byssate specimens among those collected inside hollows and crevices in hard substrata, as well as the presence of a tuft of byssus threads in specimens with regular shells lead to the conclusion that *Hiatella* and *Sphenia* living in the studied area are essentially nestling forms.

It was not possible to observe any "protective reaction" in specimens of *H. solida* and *S. antillensis* kept alive in the laboratory. Nevertheless, the reduced but evident sensitivity of the siphons when submitted to luminous and mechanical stimuli (NARCHI, 1973; NARCHI & DOMANESCHI, 1993); the great similarities in the anatomical configuration and function of the mantle, siphons, foot and byssal apparatus, along with the similar nestling habit, when compared with those in *Hiatella* studied by HUNTER (1949), lead to the conclusion that similar protective reactions indeed occur in *H. solida* and *S. antillensis*.

Retention of a small functional byssal apparatus in adults of some nestler Myoidea (*Sphenia*) and Saxicavoidea [=Hiatelloidea] (*Hiatella*), and its absence in true burrowers (except *Alolidis* Mühlfeld, 1811) in the same superfamilies, was considered by YONGE (1962) to be associated with the habit of 'nestling' in rock crevices (sometimes leading to boring) and to have been responsible for the reduction of the anterior portion of the body in relation to the posterior one leading to the asymmetry observed in these nestling species.

As the retention of a byssal apparatus functioning throughout the adult life had a major effect on the form of *H. solida* and *S. antillensis*, in accordance with the statement of YONGE (1962) about the Myoidea and Saxicavoidea [=Hiatelloidea], the nestling habit of *Hiatella* and *Sphenia* and their submission to the same selective pressures of the environment may have been responsible for the progressive evolution of similarities particularly among their shells and some pallial organs. Since *H. solida* and *S. antillensis* can be modified to suit the constraints of the habitat, it leads to the appearance of a great variability in shell form, increasing chances of superficial resemblance of one species to another.

As also occurred with *Petricola stellae* described by NARCHI (1975), for a long time misidentified as *P. pholadiformis*, *S. antillensis* may have been overlooked in the studied area in the littoral of the State of São Paulo owing to confusion with *H. solida* which it superficially resembles. The same occurred with *Sphenia binghami* from the British seas, which remained almost completely overlooked for more than half a century, i. e., since its first registers by Forbes & Hanley (1853) and Jeffreys (1865), both cited by YONGE (1951a), owing to its superficial resemblance to *Hiatella* spp. with which it normally lives.

Despite the many similarities between *H. solida* and *S. antillensis*, both species

belongs to different superfamilies in the Order Myoida Stoliczka.

At the specific level *H. solida* and *S. antillensis* can be separated in a practical way by observing the extended siphons: in *Hiatella* they are bright orange in color, relatively long, with widely separated tips while in *Sphenia* they are shorter, fused together and brownish pigmented. When the siphons are contracted or only the shell valves are available, differential features must be sought in the hinge region which shows a stout opisthodetic external ligament and short projecting teeth in *Hiatella*, while in *Sphenia antillensis* it shows an internal ligament attached to a spoon shaped chondrophore on the left valve and to an oval depression in the right valve. Similar features were pointed out by YONGE (1951a) to identify *Sphenia binghami* from *Hiatella* spp. Additional features can be found in the alimentary canal which exhibits the style-sac and midgut joined together and the stomach of type IV of PURCHON (1958) in *H. solida* while *S. antillensis* has stomach of type V of PURCHON (1960) and completely separated style-sac and midgut.

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